WIND DRIFT, LEADING LINES, AND DIURNAL MIGRATION Helmut C. Mueller and Daniel D. Berger

PERSONAL discussions with a number of North American students of bird migration indicate that there is considerable confusion and misunderstanding of the concepts of wind drift and leading lines. Recently, Murray (1964) published a review in which he refutes wind drift, at least insofar as it applies to the migration of Sharp-shinned Hawks (*Accipiter striatus*) in the northeastern United States. The present review is an attempt to: (1) define and show the implications of theories of wind drift and leading lines, in particular as to how they affect hawk migration; (2) discuss some of the evidence for the theories; and (3) show that the theories are consistent with the observations of hawk migration in the northeastern United States and show that Murray's (1964) hypothesis is inadequate. This paper is in part an attempt to extract generalizations from the available evidence. However, generalizations are rarely valid for all species and situations: and, further, generalizations based on little data are often shown to be unwarranted when more evidence becomes available.

WIND DRIFT: DEFINITION

Trowbridge (1895, 1902) may have been the first to discuss explicitly the influence of wind drift on bird migration. The theory received further analysis and support from Baxter and Rintoul (1918). There are a great number of recent works concerned with drift, and we slight many excellent papers by mentioning only Rudebeck (1950) and Williamson (1955) as examples. Lack and Williamson (1959) have defined drift as the "Displacement of a migrant from its normal route by the wind, . . ." We do not like this definition because of the implications of the adjective "normal." It is our belief that, at least for many species of migrants, drift is a normal phenomenon. We maintain that the route taken by a bird is the result of: (1) the "standard direction" (Thomson, 1953) of migratory flight: (2) wind drift, which may influence some birds more than others; and (3) at least in the case of many diurnal migrants, the topography. Data from banded birds suggest that most birds return to the same summer area year after year (Nice, 1937; Werth, 1947; Austin, 1949; Löhrl, 1959) and also that many birds return to areas in which they have previously spent the winter (Wharton, 1941; Petersen, 1953; Schwartz, 1963; Mewaldt, 1964). We know of no data, except possibly those from some species of waterfowl (see e.g. Hochbaum, 1955, p. 110-111), which offer good evidence for the hypothesis that an individual bird follows the identical migratory route year after year. We have banded over 50,000 birds at the Cedar Grove OrnithologiMueller and Berger

cal Station and have recaptured only three migrants in a subsequent season. Thus it appears that the end points of the migration are fixed and that the path pursued by a bird between these two points varies considerably from year to year. This idea was stated explicitly by Baxter and Rintoul (1918) and gains further support from current studies of the recoveries of banded birds (Mueller and Berger, in press, a,b). Since we believe that the route of a migratory bird normally is determined in part by drift, we prefer to define drift simply as the displacement of a bird due to wind.

LEADING LINES: DEFINITION AND CHARACTERISTICS

Effects of the underlying terrain on the flight of diurnal migrants have been noted by many observers. For the moment we shall restrict our attention to effects of the terrain on the direction of flight. Land birds apparently are reluctant to fly out over water and sea birds appear to be reluctant to fly in over land (van Dobben, 1953; Svärdson, 1953). Similarly, birds of open country seem to be reluctant to fly out over wooded areas and forest birds apparently are reluctant to fly out over treeless terrain (Deelder and Tinbergen, 1947; Malmberg, 1955). An isolated area of suitable habitat can attract and change the course of a diurnal migrant, acting as a "leading point" (Malmberg, 1955).

Far more important and interesting is the phenomenon of the "leading line." The leading line or *Leitlinie* was first defined by Geyr (1929). In the process of translation into Dutch, English, and other languages the meaning and definition of *Leitlinie* was altered. Some translations, such as the "diversion line" of Lack and Williamson (1959), have misleading connotations and cannot be applied readily to all types of leading lines. Geyr (1963) has authorized the following translation and definition: "Leading lines are topographical features, usually long and narrow, with characteristics that induce migrating birds to follow them. The birds are influenced by these lines in choosing their direction of flight, being so to speak led by them."

The most common type of leading line is a boundary between suitable and unsuitable habitat. The most striking example of this is a coastline, where the aversion that land birds have for water results in a concentration of migrants along the coast (Rudebeck, 1950; Mueller and Berger, 1961). Habitat boundaries, such as the edge between a forest and an open field or marsh, also act as leading lines (Geyr, 1963; van Dobben, 1955; Allen and Peterson, 1936).

Another type of leading line is that which provides conditions which expedite the passage of the birds. An outstanding example of this is the mountain ridge, which deflects the horizontal wind and provides updrafts for soaring birds (Robbins, 1956; Ulfstrand, 1960). The abundance of food

THE WILSON BULLETIN

along coasts and rivers may aid the passage of migrants that feed while migrating (von Westernhagen, 1957; Hurrel, 1955).

Lastly, there appear to be leading lines which do not border unfavorable habitat or offer any obvious advantage to the migrant except that they approximately parallel the flight direction of the bird. Examples of this include river valleys (Svärdson, 1953) and dunes and dykes (van Dobben, 1953). Thus, there is apparently a tendency for birds to follow leading lines, quite apart from the aversion of the bird to hostile habitat, or the attraction of updrafts, food abundance, or other conditions which might aid migration. Land migrants coming inland from flight over bodies of water have been observed to turn and fly along the coast (van Dobben, 1953; Lack, 1962; Williamson, 1962; Mueller and Berger, in preparation). Leading lines may help a bird orient during migration and may help it avoid excessive wind drift (Svärdson, 1953; van Dobben, 1955; Nisbet, 1957; Williamson, 1962).

EFFECTIVENESS OF LEADING LINES

A bird is, of course, not compelled to follow a leading line: it can cross, or turn back from, the line. The effectiveness of a leading line varies; some of the variables involved are listed below:

(1) The linearity of the leading line. Straight, well defined, and uninterrupted lines are most effective. An irregular and dissected coast, for example, leads few birds while a straight coastline with little variance in habitat type is highly effective (Rudebeck, 1950).

(2) The length of the leading line. The longer the line, the greater the number of birds that might encounter and follow the line.

(3) The angle formed between the leading line and the direction of flight of the bird. The greater the angle, the less the tendency for the bird to follow the line (Deelder, 1949: Svärdson, 1953).

(4) The prominence of the leading line. The coast of the ocean is obviously more effective than the shore of a narrow embayment; an abrupt, high ridge is more effective than a low, gentle slope.

(5) The bird's motivation to migrate. The higher the migratory impulse, the lower the attractiveness of the leading line (Rudebeck, 1950; Thomson, 1953).

(6) The geographic location in relation to the bird's origin and destination. Birds seem to react more strongly to the coastline in Norway, where sea crossing is undesirable, than in Holland, where sea crossing is a normal part of migration (Nisbet, 1957).

(7) Wind direction. Chaffinches (Fringilla coelebs) cross the Dutch

coast and head out over the English Channel in greater numbers in a tailwind than in a headwind (Deelder, 1949). The opposite is true for hawks crossing a strait or bay (Rudebeck, 1950; Stone, 1937).

(8) The time of day. Hawks appear to be less willing to cross water later in the day than they are early in the morning (Rudebeck, 1950).

(9) The height of flight. The greater the altitude of flight, the less the bird is influenced by leading lines (Deelder and Tinbergen, 1947; Rudebeck, 1950).

Chaffinches react to the Dutch coastline when it is up to 5 km away and when its surface subtends an angle of less than 50' (Deelder and Tinbergen, 1947). Rudebeck (1950) has observed hawks flying parallel to the Swedish coast, but some distance from it. Birds might thus follow, or parallel, a leading line at quite some distance from the line, and an observer on the line might be unaware of such a parallel flight.

HEIGHT OF FLIGHT

The height of flight of diurnal migrants influences not only their reaction to leading lines but also their probability of being observed. Some of the factors which influence height of flight are listed below:

(1) Wind direction. Birds fly higher in a tailwind and lower in a headwind or crosswind (Trowbridge, 1902; Deelder and Tinbergen, 1947; Rudebeck, 1950).

(2) Wind speed. Birds fly lower in strong winds (Deelder and Tinbergen, 1947).

(3) The underlying terrain. Sea birds fly higher over land than over the sea, land birds fly higher over the sea than over land (Svärdson, 1953). Forest birds fly higher over open, than over wooded, terrain (Deelder and Tinbergen, 1947). Hawks fly much higher over cities than over wooded terrain (Trowbridge, 1902).

(4) Leading lines. Birds flying along a leading line usually fly quite low (Deelder and Tinbergen, 1947). Hawks have been observed to descend to lower altitudes when they encounter a coast (Allen and Peterson, 1936). These observations suggest that the leading line might induce lower flight.

(5) Visibility. Chaffinches fly lower in fog and heavy rain (Deelder and Tinbergen, 1947).

EVIDENCE OF DRIFT

Most of the data in support of the theory of wind drift provide indirect evidence; it is exceedingly difficult to observe drift in progress. Before one can evaluate a direct observation which seems to indicate drift one must be certain of the following: (1) that the bird was actually migrating, (2) the standard migratory direction of the bird. (3) that the bird was not being influenced by topography. These conditions are almost impossible to meet. Whether or not a bird is actually migrating can be determined only subjectively no matter how well the migratory habits of the species observed are known, and no matter how experienced the observer. The standard migratory direction can only be inferred from the distribution of band recoveries or from observations of birds in flight, both of which are influenced by drift and topography. Attempts to determine the standard direction by experimental means may produce misleading results (see Kramer, 1950: Matthews, 1961). Absolutely featureless terrain does not exist, and the possibility that a bird is being influenced by topography cannot be dismissed completely.

With the above difficulties in mind, we submit below some observations which might be interpreted as offering some direct evidence of drift. Over the past several years we have collected 14 observations of hawks flying over relatively featureless terrain. away from obvious leading lines, and during the time of year when the species is normally migrating. Each of the hawks moved in a relatively constant direction for a considerable distance and was thought to be migrating. The 14 observations were of the following species and individuals: three Marsh Hawks (Circus cyaneus), seven Red-tailed Hawks (Buteo jamaicensis), four Rough-legged Hawks (Buteo lagopus), and more than 500 Broad-winged Hawks (Buteo platypterus). Two of the Redtailed Hawks were flying south on a calm autumn day. The Broad-winged Hawks were moving southward on an autumn day in a light northerly wind. Of the remaining individual observations, four birds were moving downwind in an inappropriate direction (at least 90° from the "expected direction" of north in spring, south in autumn). Another three birds were moving upwind in an inappropriate direction, and two birds were moving upwind in the appropriate direction. Only three birds. two low flying Marsh Hawks and one low flying Rough-legged Hawk, were observed to quarter the wind. Each of these three birds was moving in essentially the appropriate direction. The above observations suggest that some hawks fly up- or downwind. Maximum drift can occur if birds fly downwind. Considerable displacement can also occur if the birds fly into the wind. Further observations of migration away from leading lines are needed.

Rainey (1960) analyzed photographically the flight of two European Storks (*Ciconia ciconia*) over a brief interval of time and concluded that the birds were being drifted by the wind. However, the date and location of observation were not given, and it is impossible to state whether or not the birds were migrating. Lack (1960) concluded that his radar observations offered evidence for the wind drift of migrating birds. He usually found no Mueller and Berger

differences in the flight directions over land and over sea of both nocturnal and diurnal migrants.

WIND DRIFT THEORY

The lack of good, direct evidence does not prevent the elucidation of the mechanisms of drift by theoretical means. For purposes of discussion we can consider drift to be of three types: (1) Downwind drift. The birds simply fly downwind. This mode of flight has been suggested by Williamson (1955) and, somewhat differently, by Mueller and Berger (1961). (2) Free drift. The bird flies through the air in the standard migratory direction. The flight path, or track, relative to the earth is a resultant of the standard migratory direction and the wind. Lack (1960) presents evidence from radar observations which suggests that this type of drift is common over the North Sea. (3) Compensated drift. The bird attempts to compensate partially for drift by altering its direction of flight through the air so that its path relative to the earth more nearly approximates the standard migratory direction. This presumably would be very difficult without reference to landmarks. Leading lines and a low altitude of flight would aid attempts at compensation. Flight at high altitudes and with a paucity of suitable landmarks would make compensation difficult. Lack (1960), in writing of the diurnal migrations of Starlings (Sturnus vulgaris), concluded with: "Evidently, however, they can correct for drift over the land only when flying low. since radar observations in 1959 suggested that drift normally was as extensive over the land as over the sea."

Birds utilizing updrafts in flight are extremely subject to drift. In the presence of a horizontal wind, with its resulting shear, thermal updrafts are tilted downwind. Birds which soar in circles, such as hawks of the genus *Buteo*, are subject to considerable drift in the relatively slow ascent in an updraft. The direction taken in the rapid glide when the bird leaves the updraft varies with the wind direction and the orientation of leading lines. The mean flight direction resulting from several ascents and descents is not easy to discern. The flight direction in one part of such a flight pattern often is very different from the mean flight direction. More than a few students of hawk migration have been misled by this phenomenon. A detailed discussion of the action of wind drift on birds that soar in circles can be found in Rudebeck (1950).

At higher horizontal wind velocities birds no longer soar in circles. In an earlier paper (Mueller and Berger, 1961) we suggested that, at higher wind velocities, updrafts form into longitudinal strip-like cells of updrafts and downdrafts, oriented up- and downwind (see also Woodcock, 1942). Under these conditions it is considerably easier for a bird to fly up- or downwind.

than it would be for it to fly across the wind direction, and thus presumably the effects of wind drift would be increased.

Space prohibits the citation of all of the papers utilizing wind drift in the analysis of migration data. The indirect evidence for the theory of wind drift is considerable. There appears to be only one attempt at refutation of the theory, that of Murray (1964), an analysis of which follows.

WIND DRIFT AND SHARP-SHINNED HAWK MIGRATION ALONG THE NORTHEASTERN COAST OF THE UNITED STATES

In his review of studies of Sharp-shinned Hawk migration along the Atlantic coast, Murray (1964) states that: "Trowbridge (1895, 1902). Stone (1922), and Allen and Peterson (1936) hypothesized on the basis of their observations that: (1) Sharp-shinned Hawks normally migrate inland; (2) northwesterly winds drift ("lateral displacement" of Lack and Williamson, 1959) the hawks to the coast; and (3) once at the coast they continue along the coast." Our interpretation of the works of Trowbridge, Stone. and Allen and Peterson differs from that of Murray. We find that: (1) only Allen and Peterson mention the concept of a normal inland route, and it is not essential to our concept of wind drift. (2) Although Stone (1922) suggests the possibility of hawks flying along the coast, he apparently abandoned this idea in a later publication (Stone, 1937). Only Trowbridge (1895, 1902) directly mentions hawks following the coast. We quote from Trowbridge (1902): "They then turn westward and follow the Connecticut shore until they have reached New York and New Jersey, where they gradually separate and pass on southward." It would seem that Trowbridge. Stone, and Allen and Peterson were aware that hawks did not follow the coasts exactly and invariably. Murray argued that the above hypotheses were not supported by the data and offered "an alternative hypothesis that explains all of the observations."

Murray states his hypothesis in this form: "The published evidence supports the view that Sharp-shinned Hawk migration proceeds on a broad front in a generally southwestward direction (in the northeastern United States) at an altitude that makes observation difficult, and that the observed 'concentrations' or 'flights' are manifestations of the diversion line phenomenon." There is evidence that Sharp-shinned Hawks often migrate at a considerable height (Allen and Peterson, 1936), but the remaining components of Murray's hypothesis are unsupported by published evidence. The "diversion line phenomenon" is simply a variant of the leading line, in which only a portion of the birds follow the line, the remainder crossing the line. Murray's hypothesis is apparently based on the observations of a number of Dutch workers on the flight behavior of the Chaffinch and summarized by van Dobben (1953).

DIURNAL MIGRATION

The "diversion line" for hawks at Cape May differs from the Chaffinchdiversion lines in Holland in the following important characteristics: (1) It is very short: (2) Birds decrease rather than increase in numbers as one proceeds "downstream" along the line, in fact the numbers of birds appear to be at a maximum at the beginning of the diversion line; (3) The angle between the presumed migratory direction and the diversion line exceeds 90°, or, in other words, the diverted birds appear to be flying in the wrong direction along the line; (4) More birds fly out over, and across the water barrier in a head wind and more birds are "diverted" in a tail wind. These differences suggest that the concentration of hawks at the tip of Cape May is due to something other than the Murray-van Dobben model of the diversion line.

Murray postulates a broad front movement, apparently not concentrated by wind drift. Thus, we would expect similar numbers of hawks to occur over the entire northeastern United States. Local "concentrations" are thus merely the result of a *partial* diversion of the stream of migrants passing overhead. If we know the length of the "diversion line" we should be able to get a partial estimate of the numbers of birds passing overhead, and, since it is a broad-front movement, an estimate of the entire population. At Cape May, an all-autumn count taken in 1935 largely within one mile of the beginning of the "diversion line" yielded a total of 8,026 Sharp-shinned Hawks (Allen and Peterson, 1936). Probably not all of the hawks passing Cape May were counted, and, as Murray indicates, only a portion were diverted. However, let us conservatively estimate that all of the Sharp-shinned Hawks that passed over the one mile "front" at Cape May were counted in the autumn of 1935. The available information on the breeding distribution of the Sharp-shinned Hawk, and the distribution of suitable habitat, offer no reasons to believe that these hawks are more common to the northeast of Cape May than they are anywhere else in northern North America. The continent is about 2,500 miles wide. We would thus expect the North American Sharp-shinned Hawk population to be at least 20 million birds. Peterson (1948, p. 65) has estimated the total population of birds of the continent north of Mexico to number about 12 to 20 billion. It seems unlikely that one out of every 600 to 1,000 birds in North America is a Sharp-shinned Hawk. Indeed, it seems unlikely that one out of every 6.000 to 10.000 birds in North America is a Sharp-shinned Hawk. It is more reasonable to believe that the hawk observations at Cape May are of concentrations of birds, and that on the average, seen and unseen, more Sharp-shinned Hawks fly over Cape May than over most other localities.

We present below our tentative analysis of the migrations of Sharp-shinned Hawks along the northeastern coast of the United States. based on the con-

Mueller and Berger

cepts of leading line and wind drift. Concentrated flights of hawks occur only in a few localities along the Atlantic coast because the frequent embayments, marshes, irregularities, urban, and industrial areas make most of the coast a poor leading line. Both Cape May and Cape Charles are at the southern tips of huge, gradually narrowing peninsulas. The tapering forms of the Delaware-Maryland-Virginia peninsula and the New Jersey peninsula tend to funnel southbound, water-shy, diurnal migrants, in spite of the absence of good leading lines along the coasts. Concentrations of Sharp-shinned Hawks are not obvious north of Cape May and Cape Charles because (1) the frequent marshes, embayments, and tidal areas are unsuitable habitat for the hawks and they fly relatively high, and (2) the irregular borders between land, marsh, water, etc., do not form good leading lines, and hawks arriving at the coast are continually being dispersed inland. Allen and Peterson (1936) have shown that the hawks arrive at Cape May Point at considerable altitude, and that the flights north along Delaware Bay are rapidly dispersed because the hawks avoid crossing marshes and tidal creeks.

The tendency for a hawk to attempt or avoid a given water crossing is affected by a number of factors. including the bird's motivation to migrate. the time of day, and, perhaps most importantly, the wind direction. Allen and Peterson (1936) found that, at Cape May, Sharp-shinned Hawks crossed Delaware Bay when the wind was blowing from somewhere between ENE and SW and avoided the water crossing on NW to NE winds. Birds crossing Delaware Bay from Cape May often flew very high, "usually from 500 feet to the limit of vision" (Allen and Peterson, 1936). Birds avoiding the crossing also arrived at Cape May Point at a rather high altitude. dropped to a lower altitude. and moved north along the bay side of the cape (Allen and Peterson, 1936). Usually, the greatest numbers of hawks were seen at Cape May on northwesterly winds (Allen and Peterson, 1936: Stone, 1922, 1937). Good flights often occurred on southerly winds but, at least in 1935, these invariably occurred on days immediately following days of northwesterly winds. This suggests that essentially all of the major flights (excepting only two, which occurred on northerly winds) recorded by Allen and Peterson in 1935 were correlated with northwesternly winds. We believe that this correlation can be reasonably well explained by our version of the concept of wind drift. Stone (1922, 1937) also found that hawk flights at Cape May were correlated with northwesterly winds. indicating that the data of Allen and Peterson for 1935 were not peculiar.

Rusling (1937) found that the greatest flights of Sharp-shinned Hawks at Cape Charles, Virginia, in the autumn of 1936 occurred on northeasterly winds, and only small flights occurred on northwesterly winds. Murray (1964) considered Rusling's (1937) evidence and conclusions an excellent

DIURNAL MIGRATION

TABLE T Hawk Flichts on the Mid-Atlantic Coast in 1936							
Date	Wind –	Cape May		Cape Charles		Hooper Island	
		Rank	Hawks	Rank	Hawks	Rank	Hawks
25 Sept.	N–NE	1	300	6	363	1	800
13 Oct.	NE-ESE	2	174	9	246	9	75
29 Sept.	NE-ENE	3	150	10	177	-	Few
2 Oct.	N-NE	4	140	1	1,177	-	2
11 Sept.	Var.	5	120	_	**	-	aj:
19 Sept.	$\mathbf{N}\mathbf{W}$	6	110	-	\$¢	-	*
26 Sept.	E-NE	7	100	5	418	3	700
10 Sept.	NE	8	100	-	*	_	非
5 Nov.	Ν	9	90	_	24	-	0
13 Sept.	Ν	10	90	-	*	_	*
4 Oct.	ENE	-	30	2	865	-	2
5 Oct.	ENE	_	18	3	714		0
3 Oct.	NE	-	80	4	612	-	30
1 Oct.	W-N	-	8	7	359	-	0
14 Oct.	E	-	16	8	322	-	14
24 Oct.	NE–N	-	70	-	160	2	800
31 Oct.	$\mathbf{N}\mathbf{W}$	_	5	-	4	4	600
21 Sept.	NW-N	-	20	-	*	5	300
10 Oct.	SW-W	-	0	-	0	6	200
1 Nov.	SW		0	-	1	7	125
9 Nov.	NE	-	3	-	?	8	100
17 Oct.	W	-	0	-	6	10	75
12 Oct.	NW	-	30	-	134	-	0
18 Oct.	NW	-	40	-	98	-	40
30 Oct.	NW	-	0	_	5	-	50

* No data available. The data in this table are from Rusling (1937).

argument against wind drift, particularly when compared with observations from Cape May and Hooper Island, where hawks are known to occur predominately on northwesterly winds. However, in the autumn of 1936, six of the ten largest flights of Sharp-shinned Hawks at Cape May and five of the ten largest flights at Hooper Island occurred on days with northeasterly winds (Table 1). The fact that nine of the ten largest flights at Cape Charles occurred on northeasterly winds is not remarkable when compared with the above. At least the three greatest counts of Sharp-shinned Hawks for 1936 occurred on northeasterly winds in all three of the above localities (Table 1). It is remarkable that the highest counts of Sharp-shinned Hawks at Hooper Island and Cape May occurred on northeasterly winds rather than, as in previous years, on northwesterly winds. It is further interesting that only 2.269 Sharp-shinned Hawks were seen at Cape May in 1936 (Rusling, 1937), as compared with 8,206 in 1935, 5,675 in 1932, and 10,000 in 1931 (Allen and Peterson, 1936). Strong northwesterly winds and clear skies prevailed on only three days during September and October 1936 at Cape Charles (Rusling, 1937). These conditions usually produce great numbers of hawks at Cape May and, presumably, at Hooper Island (Allen and Peterson, 1936). On all of these days relatively few Sharp-shinned Hawks were seen at Cape May, Hooper Island, and Cape Charles, but greater numbers were seen at Cape Charles than at the other two localities on two of the three occasions (Table 1). In all, 1936 seems to have been a very unusual autumn for hawk migration along the mid-Atlantic coast of the United States. It would be interesting to see the characteristics of the Sharp-shinned Hawk migration at Cape Charles in a more usual year.

Because of the configurations of the peninsulas, we would expect concentrations of hawks at Cape May and Cape Charles in autumn if three conditions prevail: (1) reasonable numbers of hawks exist on. or arrive on. the New Jersey and Delaware-Maryland-Virginia peninsulas, (2) the birds migrate in some southerly direction, and (3) the birds exhibit some reluctance to cross bodies of water. We have previously discussed the third factor and the second safely can be assumed to occur. The first factor, however, can be analyzed only indirectly. The interaction of wind and leading lines in affecting the flight paths of hawks in the areas north of the New Jersey and Delaware-Maryland-Virginia peninsulas undoubtedly plays a major role in determining the abundance of hawks on the peninsulas. The strong leading lines provided by the Appalachian ridges lie but a short distance to the west of the Atlantic coast: and. farther to the north, the Great Lakes and the Gulf of St. Lawrence probably affect the flight paths of hawks. The frequent embayments on the coast and gaps in the ridges of the Appalachians add further complications. More observations of hawk migration at localities north and west of the coastal concentration points are needed before all questions can be answered. However, it is interesting to note that 4.611 Sharp-shinned Hawks, or 67 per cent of the total observed at Cape Charles. were counted in the two periods between 1 and 5 October, inclusive, and 12-15 October, inclusive. Both of these periods began with, or were preceded by, at least one day of westerly winds over the entire region (Rusling. 1937). We believe that this suggests that wind drift may have been a factor in bringing hawks to the Delaware-Maryland-Virginia peninsula, and, once there, they continued southward to Cape Charles, producing concentrations at the cape for several subsequent days.

In addition to the above, we would expect differences in the flights at Cape May and Cape Charles because (1) the New Jersey peninsula has a relatively broad base whereas the Delaware-Maryland-Virginia peninsula has a relaMueller and Berger

tively narrow connection with the mainland, (2) Chesapeake Bay is longer and generally wider than Delaware Bay, and (3) Cape Charles is about four times as long as Cape May and is extremely narrow at several points considerable distances from the tip.

In conclusion, we fail to see how Murray (1964) has produced any evidence which can be used to argue that wind drift is not a factor in producing concentrations of Sharp-shinned Hawks at selected points on the coast of the northeastern United States. The alternative hypothesis proposed by Murray is unsupported by, and inconsistent with, the available evidence.

SUMMARY

This paper attempts to: (1) define the concepts of wind drift and leading lines, (2) present the characteristics of each of these phenomena, (3) elucidate the various factors influencing wind drift and leading line behavior, and (4) document the above with a brief review of the literature of migration. In addition, the hypothesis of Murray (1964) is critically evaluated as an alternative to wind drift theory and rejected as being inconsistent with available information.

ACKNOWLEDGMENTS

This paper began as the discussion section of an early draft of a research report on Sharp-shinned Hawk migration at Cedar Grove, Wisconsin (Mueller and Berger, in press, b). Financial support for the latter study was provided by the National Science Foundation (Grant GB-175). We are indebted to Professor John T. Emlen for advice and assistance in various aspects of the study.

LITERATURE CITED

Allen, R. P., AND R. T. PETERSON

1936 The hawk migrations at Cape May Point, New Jersey. Auk, 53:393–404. AUSTIN, O. L.

1949 Site tenacity, a behaviour trait of the Common Tern (Sterna hirundo Linn.) Bird-Banding, 20:1-39.

BAXTER, E. V., AND L. J. RINTOUL

1918 The birds of the Isle of May: a migration study. *Ibis*, 6, *ser*. 10:247–287. DEELDER, C. L.

1949 On the autumn migration of the Scandinavian Chaffinch, (Fringilla c. coelebs L.). Ardea, 37:1–88.

DEELDER, C. L., AND L. TINBERGEN

1947 Waarnemingen over de vlieghoogte van trekkende Vinken, Fringilla coelebs L., en Spreeuwen, Sturnus vulgaris L. Ardea, 35:45-78.

DOBBEN, W. H. VAN

1953 Migration in the Netherlands. Ibis, 95:212-234.

1955 Nature and strength of the attraction exerted by leading lines. Acta XI Congr. Internatl. Ornith. Basel:165-166.

GEYER VON SCHWEPPENBURG, H. FRIEH.

1929 Zugstrassen-Leitlinien. J. Ornith., Ergänzungsband II:17-32.

1963 Zur Terminologie und Theorie der Leitlinie. J. Ornith., 104:191-204.

Носнваим, Н. А

1955 Travels and traditions of waterfowl. U. Minnesota Press, Minneapolis.

HURREL, H. G.

1955 Simultaneous migration watches for Swifts in the British Isles. Acta XI Congr. Internatl. Ornith. Basel:640-642.

KRAMER, G.

1950 Weitere Analyse der Faktoren, welche die Zugaktivität des gekäfigten Vogels orientieren. *Naturwiss.*, 37:377-388.

Lack, D.

1960 Migration across the North Sea studied by radar. Part 2. The spring departure 1956–59. *Ibis*, 102:26–57.

1962 Radar evidence on migratory orientation. Brit. Birds, 55:139-158.

LACK, D., AND K. WILLIAMSON

1959 Bird-migration terms. Ibis, 101:255-256.

Löhrl, H.

1959 Zur Frage des Zeitpunktes einer Prägung auf die Heimatregion beim Halsbandschnäpper (*Ficedula albicollis*). J. Ornith., 100:132-140.

MALMBERG, T.

1955 Topographical concentration of flight lines. Acta XI Congr. Internatl. Ornith. Basel:161-164.

MATTHEWS, G. V. T.

1961 'Nonsense' orientation in Mallard and its relation to experiments in bird navigation. *Ibis*, 103a:211-230.

MEWALDT, L. R.

1964 California sparrows return from displacement to Maryland. Science, 146: 941-942.

MUELLER, H. C., AND D. D. BERGER

- 1961 Weather and fall migration of hawks at Cedar Grove, Wisconsin. Wilson Bull., 73:171-192.
- in press, a. "Navigation" of hawks: evidence from spring migration observations and band recoveries.
- in press, b. Migration of Sharp-shinned Hawks: analysis of data from Cedar Grove, Wisconsin.

in preparation. Analysis of concentrations of nocturnal migrants along a coastline. MURRAY, B. G., JR.

1964 A review of Sharp-shinned Hawk migration along the northeastern coast of the United States. Wilson Bull., 76:257-264.

NICE, M. M.

1937 Studies in the life history of the Song Sparrow. I. Trans. Linnaean Soc. New York, 4:1-247.

NISBET, I. C. T.

1957 Passerine migration in South Scandinavia in the autumn of 1954. *Ibis*, 99: 228-268.

PETERSEN, E.

1953 Orienteringsforsøg med Haettemage (Larus r. ridibundus L.) og Stormmage (Larus c. canus L.) vinterkvarteret. Dansk Ornithol. Forenings Tidsskrift, 47:153-178.

PETERSON, R. T.

¹⁹⁴⁸ Birds over America. Dodd, Mead, New York.

RUSLING, W. J.

1937 The study of the habits of diurnal migrants, as related to weather and land masses during the fall migration on the Atlantic coast, with particular reference to the hawk flights of the Cape Charles (Virginia) region. Unpublished manuscript in the library of the National Audubon Society, New York.

Schwartz, P.

1963 Orientation experiments with Northern Waterthrushes wintering in Venezuela. Proc. XIII Internatl. Ornith. Congr. 481–484.

STONE, W.

1922 Hawk flights at Cape May Point, N. J. Auk, 39:567-568.

1937 Bird studies at old Cape May, Vol. 1. Delaware Valley Ornith. Club, Acad. Nat. Sci. Philadelphia.

Svärdson, G.

1953 Visible migration within Fenno-scandia. Ibis, 95:181-211.

THOMSON, SIR A. L.

1953 The study of the visible migration of birds. *Ibis*, 95:165–180.

TROWBRIDGE, C. C.

1895 Hawk flights in Connecticut. Auk, 12:259-270.

1902 The relation of wind to bird migration. Amer. Nat., 36:735-753.

ULFSTRAND, S.

1960 Migration of African kites Milvus migrans (Bodd.)—M. aegyptius Sharpe & Bouvier, and Wahlberg's Eagles Aquila wahlbergi Sund., at Lake Tanganyika. Kungl. Fysiografiska Sällskapets I Lund Förhandlingar, 30:31-39.

Werth, I.

1947 The tendency of Blackbird and Song Thrush to breed in their birthplaces. Brit. Birds, 40:328-330.

WESTERNHAGEN, W. VON

1957 Planbeobachtungen des Vogelzuges Herbst 1955. Mitt. Faun. Arbeitsgem. Schleswig-Holsteins. 10:17-55.

WHARTON, W. P.

1941 Twelve years of banding at Summerville, S. C. Bird-banding, 12:137-147. WILLIAMSON, K.

1955 Migrational drift. Acta XI Congr. Internatl. Ornith. Basel:179-186.

1962 The nature of 'leading line' behavior. Bird Migration 2:176-182.

WOODCOCK, А. Н.

1942 Soaring over the open sea. Sci. Mon., 55:226-232.

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RAINEY, R. C.

¹⁹⁶⁰ Applications of theoretical models to the study of flight-behavior in locusts and birds. Symposia Soc. for Expl. Biol., XIV:122-139.

ROBBINS, C. S.

¹⁹⁵⁶ Hawk watch. Atlantic Naturalist, 11:208-217.

RUDEBECK, G.

¹⁹⁵⁰ Studies on bird migration. Var Fagelvärld, Supplementum I.